A new species of *Lucinoma* from 240–500 m on the continental shelf break off Newfoundland (Bivalvia: Lucinidae)

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ABSTRACT

A new species of the lucinid bivalve genus *Lucinoma* is described from shells dredged at depths of 240–500 m from the edge of the continental shelf off southern Newfoundland. It differs from the other northern species, *Lucinoma filosa*, in shape, ligament, and characters of the anterior adductor muscle scar. It also differs from the poorly known *Lucinoma atlantis* from the outer shelf off Maryland that is longer than high and has both anterior and posterior sulci, and from *L. blakeana* from deep water off North Carolina, a smaller species with a truncate posterior margin. Other *Lucinoma* species are recorded further south in the northern Gulf of Mexico, particularly from hydrocarbon seeps, although the taxonomy is confused for those taxa.

INTRODUCTION

The chemosymbiotic Lucinidae is now recognized as one of the most speciose of marine bivalve families (Huber, 2015; WoRMS) and further new species and genera continue to be described (Glover and Taylor, 2016). *Lucinoma*, with at least 30 living species, is the best known and widespread of the deeper-water lucinid genera. The genus has a latitudinal range from 70° N to 55° S and from the intertidal zone to deeper than 2500 m (summary figure in Taylor and Glover, 2010, fig 5.9). The majority of *Lucinoma* species are found from >200 m to mid-bathyal depths and are often abundant at hydrocarbon seeps, mud volcanoes and oxygen minimum zones (Cary et al., 1989; Okutani and Hashimoto, 1997; Callender and Powell, 1997, 2000; Salas and Woodside, 2002; Olu-Le Roy et al., 2004; Holmes et al., 2005; Cosel, 2006; Cosel and Bouchet, 2008; Oliver and Holmes, 2006; Duperron et al., 2007; Oliver et al., 2012; Zamorano and Hendrickx, 2012). Around 40% of *Lucinoma* species have been described within the last 15 years suggesting that diversity has not yet been fully sampled. Nonetheless, it should be noted that some *Lucinoma* species reported from Japan (Okutani and Hashimoto, 1997), *L. adamsiana* Habe, 1958 and *L. japonica* Habe, 1958, are now classified in other genera and subfamilies (Glover and Taylor, 2016).

The phylogenetic placement of *Lucinoma* has been problematic. An initially surprising result from molecular analyses of Lucinidae was that *Lucinoma* species grouped within a major clade (subfamily Codakiinae) of otherwise largely shallow water species of *Ctena* and *Codakia* (Taylor et al., 2011; 2014; 2016). Previously, using shell characters, Dall (1901) had classified *Lucinoma* as a subgenus of *Phacoides*, a placement also followed by Britton (1970). By contrast, Chavan (1938; 1969) considered the genus to be related to *Myrtea* and placed it in the Myrteinae (also Abbott, 1974), while Bretsky (1976) classified it as a subgenus of *Miltha*. At species level *Lucinoma* are difficult to discriminate, but useful shell characters are: overall shape, form of commarginal sculpture, presence of posterior and anterior sulci, thickness of hinge line and size of cardinal teeth, presence/absence of anterior lateral teeth, and in particular, characters of the anterior adductor muscle scar, notably the length, width and angle of ventral detachment from the pallial line.

On the western Atlantic continental margin three species of *Lucinoma* have been described: *Lucinoma filosa* (Stimpson, 1851), *L. blakeana* (Bush, 1893), and *L. atlantis* (McLean, 1936). Unfortunately, only dead shells are available for study and no *Lucinoma* species from the Western Atlantic have been included in molecular analyses. Recently, we located in the collections of the Muséum national d'Histoire naturelle, Paris, several samples of a *Lucinoma* species collected in 1985 from dredging on the edge of the continental shelf off southern Newfoundland. These shells had been labelled as *Lucinoma filosa*, but differed from that species and also from the two other *Lucinoma* species described from the northwestern Atlantic. The samples were obtained during a survey of fish stocks (ERHAPS 851) in the territorial waters of Saint-Pierre and Miquelon, a small archipelago of French territory (*Collectivité d'Outre-mer de Saint-Pierre-et-Miquelon*) off the southern coast of Newfoundland. A narrow strip (10.5 nautical miles wide) of territorial waters (Exclusive Economic Zone) extends southwards across the continental shelf. Cosel (1986)

published a semi-popular account of the ERHAPS 851 cruise and a list of the mollusks recovered. In this paper we describe this new species of *Lucinoma* and compare it with congeners from the region.

MATERIALS AND METHODS

The length of anterior adductor muscle scars in relation to shell height and length were measured on shells using calipers, while measurements from *L. filosa* were mainly taken from scaled images of shell interiors from specimens in ANSP, USNM, and MCZ (latter images courtesy of G. Giribet and A. Baldinger). Similar measures were made from images of the holotypes of *L. blakeana* and *L. atlantis*. Outline drawings of shell interiors were made from digital images using Photoshop.

Institutional acronyms used: ANSP, Academy of Natural Sciences Philadelphia at Drexel University, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, The Natural History Museum, London, U.K.; USNM, United States Museum of Natural History, Washington, USA. Other abbreviations: aas, anterior adductor muscle scar; fms, fathoms; H, shell height; L, shell length; LV, left valve; pv, paired valves; RV, right valve; v, single left or right valve.

SYSTEMATICS

Bivalvia
Family Lucinidae Fleming, 1828
Subfamily Codakiinae Iredale, 1937

Genus *Lucinoma* Dall, 1901

Type Species: *Lucina filosa* Stimpson, 1851 Original designation

Description: Medium to large shells. Subcircular to anteriorly tapering. Posterior sulcus with marginal sinus present in some species, anterior sulcus rarely present. Sculpture of narrow, regularly spaced, commarginal lamellae with finer lamellae between, radial sculpture absent. Lunule lanceolate, slightly sunken. Ligament long, external, protruding or in groove. Hinge with two cardinal teeth in each valve, larger teeth usually bifid, small to obscure anterior lateral teeth. Anterior adductor muscle scar usually long and detached from pallial line for about ¾ of length. Inner shell margin smooth.

Lucinoma thula new species
(Figures 1–13, 14–15)

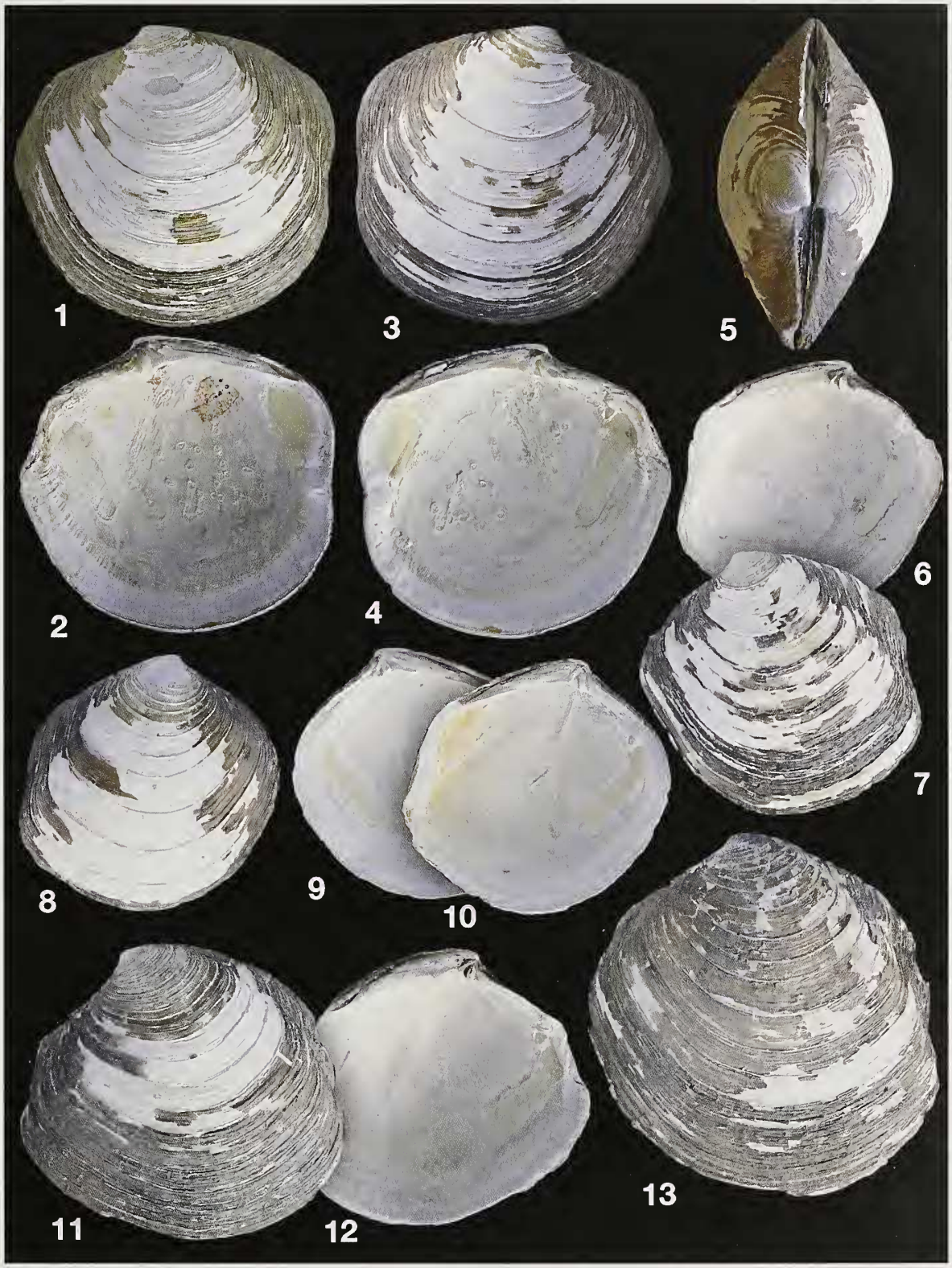
Description: L to 70 mm, H to 63 mm, slightly longer than high (H/L=0.94±0.04, SD, n=28). Robust, subcircular, shallow posterior sulcus, posterior margin truncate with shallow sinus, anterior margin slightly projecting, ventral margin broadly rounded. Umbones broad, low, prosogyrate. Periostracum: thick, dark olive-brown. Sculpture: widely spaced, low, sharp, commarginal lamellae with 5–7 finer commarginal "cords" in interspaces. Major lamellae are more closely spaced ventrally in larger shells. Lunule: long, lanceolate. Ligament: external, long, set on nymph. Hinge: RV with two cardinal teeth, anterior thin, posterior larger, slightly bifid, lateral teeth absent; LV with two cardinal teeth, anterior larger, slightly bifid. Anterior adductor muscle scar long, ventrally detached from pallial line at an angle of about 20°; posterior adductor scar ovoid, anterior pedal retractor muscle scar separate and dorsal to anterior adductor scar. Pallial line entire, shell within line with subcircular scars of mantle attachment, pallial blood vessel trace visible, inner shell margin smooth.

Type Material: All type material from ERHAPS 851 cruise N.O. CRYOS; **Holotype:** One whole shell, Station L219, 345–512 m, 45°01' N, 54°57' W, 09 March 1985, L=61.3 mm, H=58.1 mm, tumidity single valve=15.2 mm, MNHN IM-2000-33102; **Paratypes:** MNHN IM-2000-33103, station L181, 310–308 m, 46°32' N, 57°31' W, 01 March 1985, 6 RV 9 LV (L=69.8, 57.2, 50.8, 54.8, 47.0, 45.8, 44.5, 40.3, 33.5 mm); MNHN IM-2000-33104, station L184, 243–244 m, 46°21' N, 57°21' W, 01 March 1985, 1 LV (L=55.6 mm); MNHN IM-2000-33105, station L185, 314–320 m, 46°18' N, 57°22' W, 01 March 1985, 1RV, 1LV, (L=53.5, 53.3 mm); MNHN IM-2000-33106, station L186, 282–278 m, 46°12' N, 57°17' W, 01 March 1985, 2 RV, 3LV (L=65, 55.2, 52.6, 51,5, 49,7 mm); MNHN IM-2000-33107, station L187, 323–322 m, 46°05' N, 57°12' W, 01 March 1985, 9 LV, 5 RV (L=56.3, 55.6, 52.8, 48.3, 47.7, 46.1, 44.6, 42.2, 42.1, 40.1, 37.9 mm); MNHN IM-2000-33108, station L189, 332–320 m, 46°60' N, 57°04' W, 02 March 1985, 2 pv (L=53.4, 36.6 mm); NHMUK 20170141, station L187, 323–322 m, 46°05' N, 57°12' W, 01 March 1985, two single valves (L=46.9, 44.3 mm).

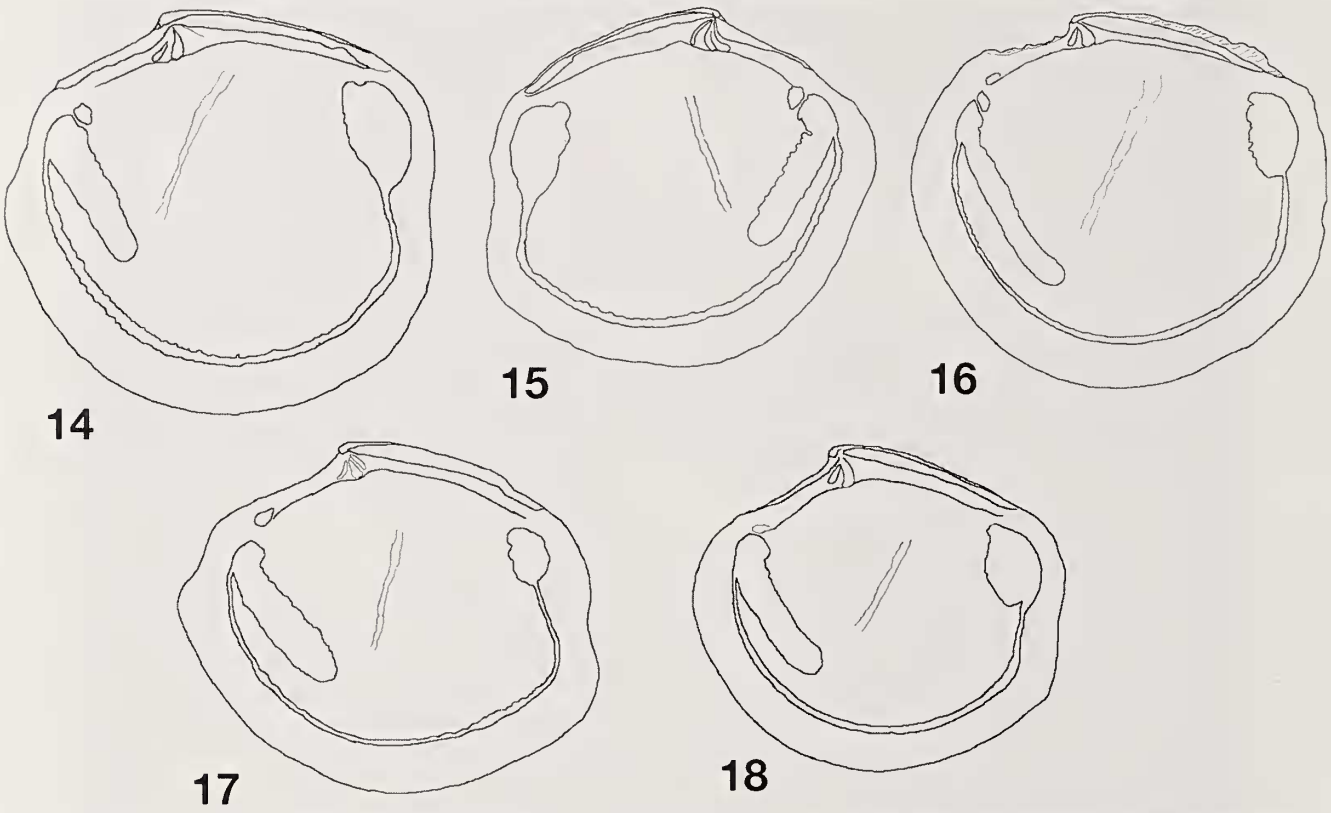
Habitat: Recorded from depths of 240–512 m near the edge of the continental shelf off southern Newfoundland. Rudo von Cosel (personal communication) reported that the sediment was fine to coarse sand and the accompanying fauna comprised "...regular sea urchins, lots of ophiurids, a few shrimps and large actinias, and among the mollusks mostly Buccinidae of different genera and species (17 in total)." See Cosel (1986) for a list of other mollusks recovered from the ERHAPS cruise but without details of individual stations.

Etymology: Derived from Latin *thule* for furthest north, in reference to the northerly location of the species.

Comparison with Other Species: The three *Lucinoma* species previously described from the northwestern Atlantic are illustrated in Figures 19–31 and their principal features documented below. The type localities of the northwestern Atlantic species are plotted in Figure 33.



Figures 1–13. *Lucinoma thula* new species, all specimens from ERHAPS 851 cruise. **1–5.** Holotype (MNHN IM-2000-33102), station L219, L=61.3 mm. **1–2.** Exterior and interior of left valve. **3–4.** Exterior and interior of right valve. **5.** Dorsal view. **6–7.** Paratype (NHMUK 20170141), station L187, interior and exterior of left valve, L=56.1 mm. **8–10.** Paratype (MNHN IM-2000-33103), station L181, exterior of right valve and interior of right and left valves, L=38.3 mm. **11–12.** Paratype (MNHN IM-2000-33106), station L186, exterior and interior of left valve, L=50.9 mm. **13.** Paratype (MNHN IM-2000-33106), station L 186, exterior of left valve, L=64.1 mm.



Figures 14–18. Internal drawings of valves. **14–15.** *Lucinoma thula* new species. **14.** Holotype **15.** Paratype (NHMUK 20170141). **16.** *L. filosa* (ANSP 102172). **17.** *L. atlantis*, holotype. **18.** *L. blakeana*, holotype.

***Lucinoma filosa* (Stimpson 1851)**
(Figures 16, 19–24, 34–35)

Brief Description: Shell length to 60 mm, subcircular, slightly longer than high (H/L=0.88±0.02 SD, n = 12), sculpture of regular, sharp commarginal lamellae. Slight posterior and anterior sulci. Lunule long, slightly sunken, Anterior dorsal margin elevated. Ligament in a groove with a deep escutcheon. Two cardinal teeth and vestigial anterior lateral tooth in each valve. Anterior adductor muscle scar very long and narrow, detached from pallial line for 4/5 of length (details below Figure 32). Periostracum relatively thin, pale tan, or buff.

Type Material: Not located (see Britton 1970, Bretsky 1976). The type locality (Stimpson, 1851:17) is cited as "...in 6 f sand near Pt Shirley (W.S.), Phillips Beach, alive after a storm (Holder)". Point Shirley is now in the town of Winthrop, a suburb of Boston, Massachussetts.

Distribution: *Lucinoma filosa* is distributed from Canada to Florida Keys and maybe into the Gulf of Mexico. It is well represented in collections from northern areas with recorded depths of 20–80 m but occurs in deeper water (to 400 m) further south off Florida Keys (Britton, 1970) (NHMUK20140794, see Figure 34–35). It was also recorded as common on the continental shelf in the Middle Atlantic Bight area, in less than 200 m, between Cape Cod and Cape Hatteras (Wigley and Theroux, 1981: 95, fig. 76).

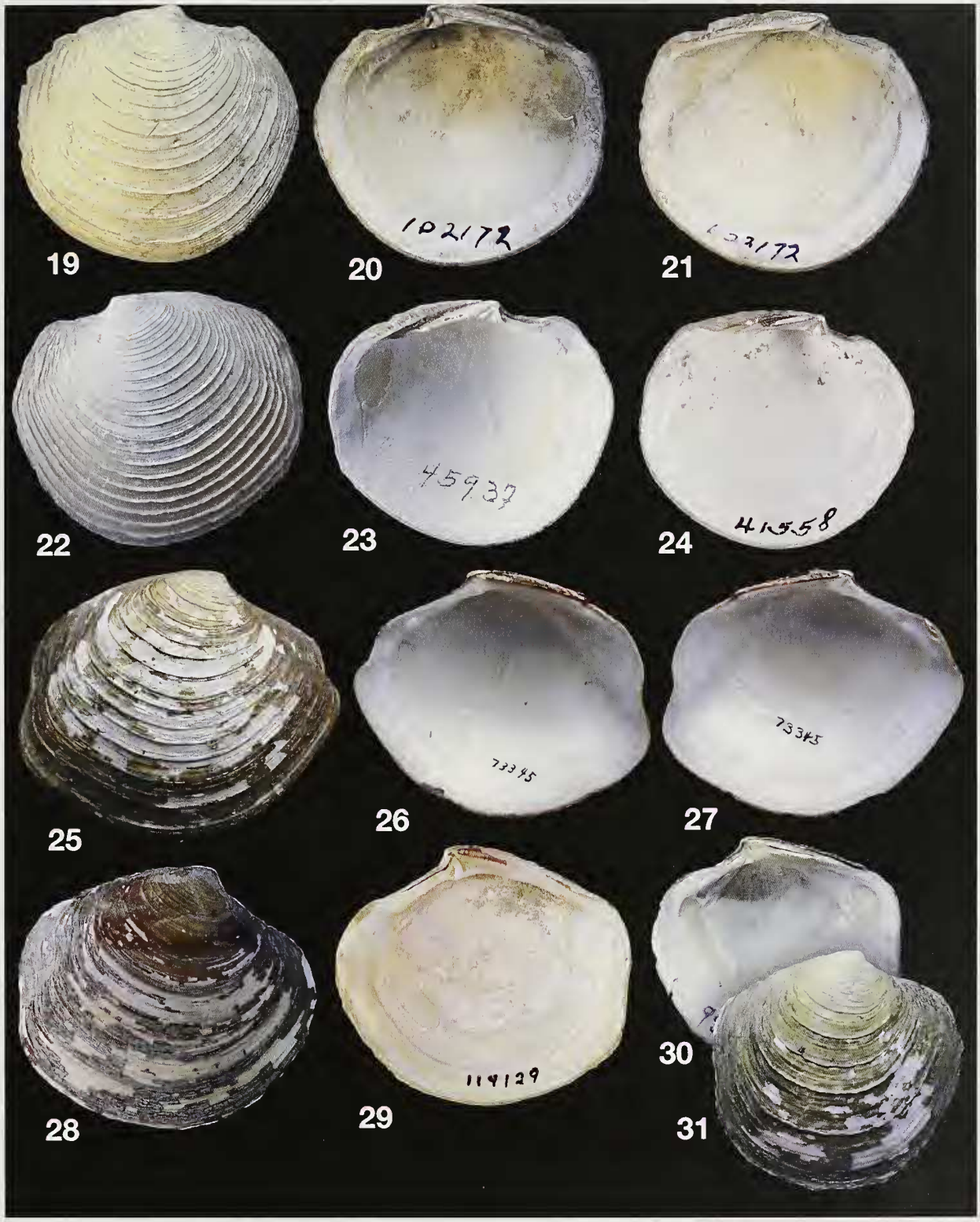
***Lucinoma atlantis* (McLean, 1936)**
(Figures 17, 25–27)

Brief description: Holotype is longer than high, H/L=0.81, with widely spaced thin commarginal lamellae. Prominent anterior sulcus and posterior sulcus with marginal sinus. Larger of the two cardinal teeth bifid, distinct anterior lateral teeth in both valves. Anterior adductor muscle scar long, detached from pallial line for ¾ of length. Periostracum thick and olive brown.

Type Material: Holotype, MCZ 73345, PV L=58.3 mm, H=47.3 mm

Type Locality: Off Maryland, 216–549 m, 38°10' N, 73°51' W (note coordinates on holotype label are incorrect) at edge of continental shelf.

Distribution: Known only from the holotype and we have seen no other comparable material. Bivalves identified as this species are widely reported from sites of hydrocarbon seeps off Louisiana in the northern Gulf of Mexico (Figures 39–46) (Turner, 1985: fig 2H; MacDonald et al., 1990; Callender et al., 1990; Callender and Powell, 1997) but specimens we have examined from



Figures 19–31. *Lucinoma filosa*, *L. atlantis* and *L. blakeana*. **19–21.** *Lucinoma filosa*, off Martha's Vineyard (ANSP 102172), L=39.4 mm. **22–23.** *L. filosa* (USNM 45937) exterior and interior of left valve, off Martha's Vineyard, 144 m, USFC stn 941, L=47 mm. **24.** *L. filosa* (MCZ 41558), interior of left valve, off New Jersey, 40° 01' N, 70°30' W, 225 m, L=30.3 mm. **25–27.** *Lucinoma atlantis*, holotype (MCZ 73345) exterior of right valve and interior of right and left valves, off Maryland, 216–549 m, 38°10' N, 75° 51' W, L=58.3 mm. **28–29.** *Lucinoma blakeana*, holotype (MCZ 119129), exterior and interior of right valve, off Cape Fear, North Carolina, 464 fms (850 m), Blake station 326, 33°42'15" N, 76 °00'50" W, L=30 mm. **30–31.** *L. blakeana* (USNM 95694), exterior and interior of left and right valves, ALBATROSS Station 2677, 874 m, off Cape Fear, 32°39' N, 76°50' W, L = 41.6 mm.

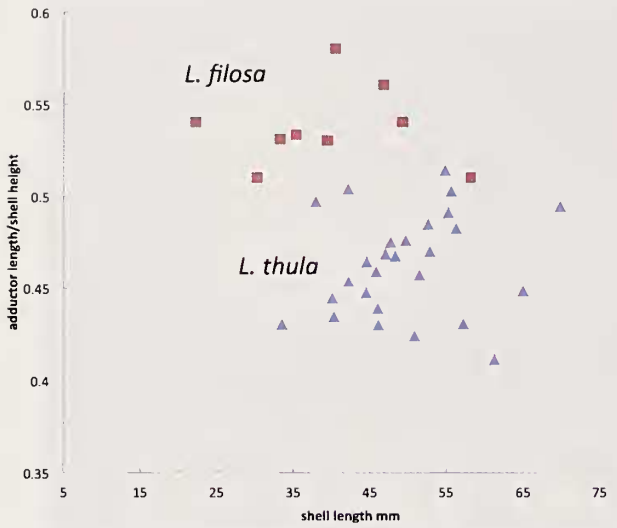


Figure 32. Comparison between *Lucinoma thula* and *L. filosa* in the relative length of the anterior adductor muscle scar (length of aas/shell height) plotted against shell length.

this region differ from the holotype of *L. atlantis* (despite the opinion of Turner, 1985) in lacking the anterior sulcus and thick, dark periostracum and likely represent a separate species.

Lucinoma blakeana (Bush, 1893)

(Figures 18, 28 –31, 36 –38)

Type Material: Holotype MCZ 119129, single RV L=30.1 mm, H=26.9 mm, H/L=0.86.

Type Locality: Off Cape Fear, North Carolina, 850 m, Blake Expedition, 1880, station 326, 33°42' 15" N, 76°00'50' W.

Brief Description: Small species L to 30 mm longer than high, H/L=0.86, with a distinctive quadrate posterior margin and shallow posterior sulcus. Sculpture of widely spaced, thin, commarginal lamellae. Lunule long and lanceolate. Small anterior lateral teeth present in both valves and two cardinal teeth, larger bifid. Anterior adductor muscle scar long, ventrally detached from pallial line for ¾ of length. Periostracum of holotype is now tan brown but it was originally described (Bush, 1893) as thin and light yellow.

Distribution: Other specimens, also from off Cape Fear are USNM 92670, Albatross station 2628, 966 m, and USNM 95694, Albatross station 2677, 874 m, and similar shells are recorded from off Havana (Figures 36–38), USNM 64435, Blake station 43, on label as 24°08' N, 82°51' W, 449 fms (821 m); but the Blake station list in USNM records 339 fms (620 m) and 83°51' W for station 43. The few confirmed records available suggest that this is a much deeper water species than *L. filosa* and *L. thula*.

Remarks: A further *Lucinoma* species is represented by some shells from the northern Gulf of Mexico collected from Viosca Knoll lease block 826 (29°09' N, 88°01' W, depth ca. 450 m, off Alabama) and sent to Ruth Turner for identification (MCZ). These are illustrated in Figures 47–50. This is a large (L=81 mm, H=80 mm), rounded, inflated species, without significant sulci and with low commarginal lamellae that are much more closely spaced than the other *Lucinoma* from the northwestern Atlantic. The cardinal teeth are large with a small anterior lateral tooth in the left valve and the anterior adductor muscle scar is medium-length and broad. This species differs from the putative *L. atlantis* of the Gulf of Mexico and other western Atlantic *Lucinoma* species in shape, lack of sulci and the closely spaced lamellae. The taxonomy of all the *Lucinoma* species recovered from hydrocarbon seeps in the Gulf of Mexico remains problematic.

One of the main features that differentiates the new species, *Lucinoma thula*, from *L. filosa* is the length and position of the anterior adductor muscle scar; this is long and narrow in *L. filosa*, lying approximately parallel with the pallial line (Figure 16) and ventrally detached for 4/5 of length at an angle of about 12°. By comparison, in *L. thula* the adductor scar is shorter, broader, and diverges from the pallial line at an angle of about 20°. The relative lengths of the anterior adductor scar (as length/shell height) were compared: mean 0.46±0.3 SD, n=27 for *L. thula* and 0.53 ± 0.2 SD, n=11 for *L. filosa* (Figure 32). These were significantly different (T test, p >0.05). *Lucinoma filosa* has more closely spaced commarginal lamellae and is subcircular in outline but *L. thula* is posteriorly truncate. In most shells of *L. filosa* the posterodorsal shell margin extends above the ligament (Figures 19–24), but not in *L. thula*. The periostracum is thicker and dark in *L thula* compared to the pale and relatively thin periostracum of *L. filosa*.

The holotype of *Lucinoma atlantis* differs from *L. thula* in its markedly longer than high shell outline, distinct anterior and posterior sulcus (Figures 25–27), and visible anterior lateral teeth in both valves. *Lucinoma blakeana* is a smaller species (Figures 28–29) that differs in shape from *L. thula* and *L. filosa* with a quadrate posterior margin, only a slight posterior sulcus and a tan brown or yellowish periostracum compared with the darker olive brown of *L. thula* and *L. atlantis*.

DISCUSSION

It is probable that *Lucinoma thula* has been confounded with *L. filosa* in faunal surveys of the outer continental shelf and upper slope of the northwestern Atlantic but we have seen no other specimens in MCZ, ANSP, or USNM collections. From a macrobenthic survey of the northeastern USA continental shelf and slope, Theroux and Wigley (1998) recorded *L. filosa*, *L. blakeana* and *Lucinoma* sp. but gave no images or details.

Ideally, the taxonomic discrimination of *Lucinoma* species should be corroborated with molecular data. To

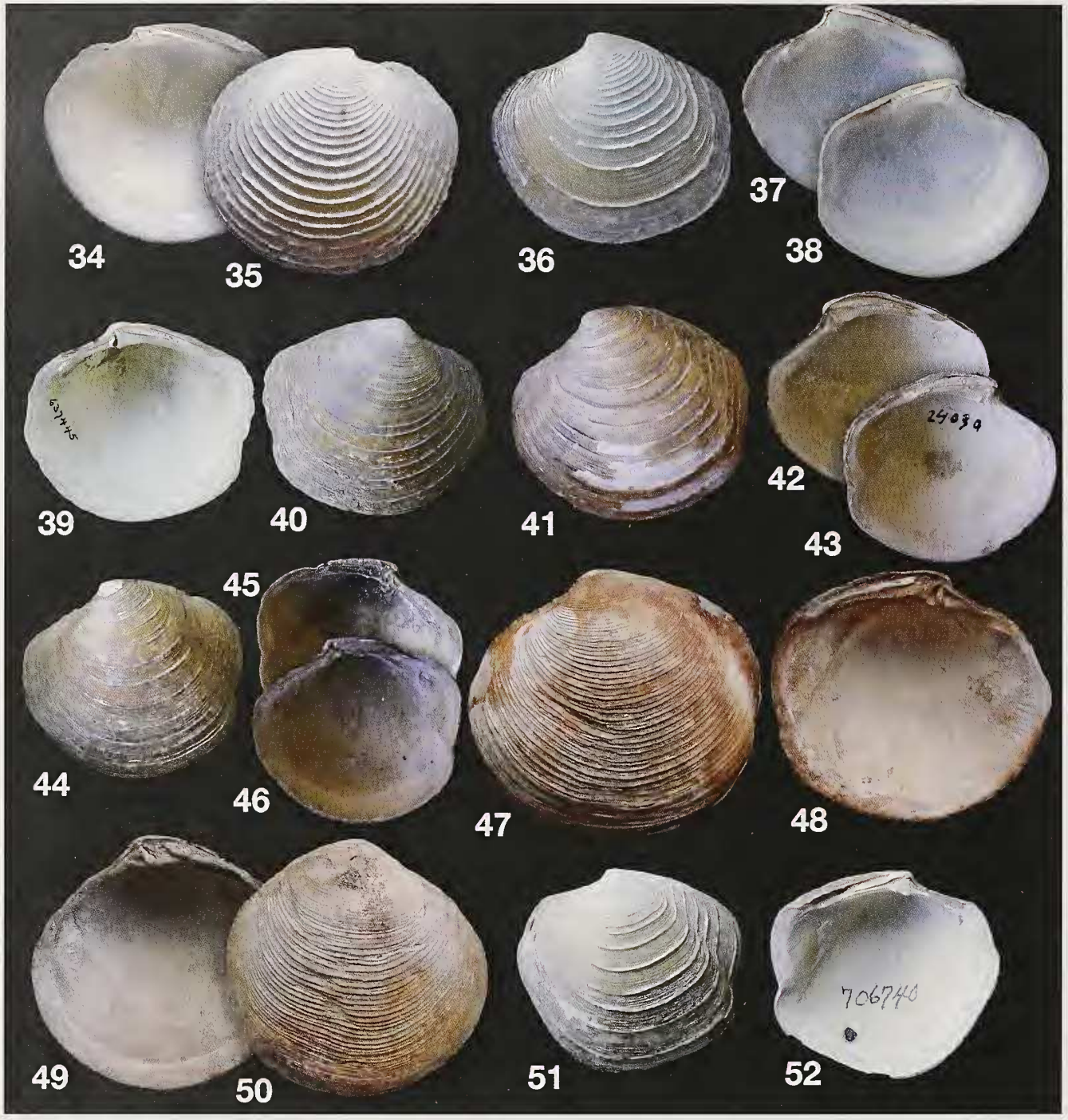
Figure 33. Map showing type localities of the *Lucinoma* species described from the eastern Atlantic seaboard of North America, and locations in the Gulf of Mexico of shells illustrated in Figures 34–52. Map from Google Earth Image 2017.

date only six species of *Lucinoma* have been included in molecular analyses; these originated from widely separated locations and depths but with none from the northwestern Atlantic. The species group in a well-supported clade with short branches and form a sister group to *Codakia* species (Taylor et al., 2016). Inclusion of the type species, *Lucinoma filosa*, and the other species from the western Atlantic is highly desirable. Nevertheless, the new species *L. thula* clearly differs morphologically from *L. filosa* and we are confident of its distinct identity. The northeastern Pacific species *Lucinoma annulata* (Reeve, 1850) has similar shape, sculpture, and musculature to *L. filosa* and may be a sister taxon. This species likewise occurs in shallow subtidal habitats at the northern end of its range in Alaska and in deeper water (665 m) at more southerly locations off Mexico (Coan et al., 2000). Described from a methane seep area in the eastern Pacific Ocean off Concepcion, Chile, *Lucinoma anemiophila* (Holmes, Oliver, and Sellanes, 2005) has a general similarity to *L. thula* but with more prominent anterior lateral teeth.

Recent surveys have revealed the presence of numerous sites of seafloor methane leakage along the northern US Atlantic margin (Skarke et al., 2014) and cold seep communities reported at depths as shallow as 400–430 m in the Baltimore Canyon (http://oceanexplorer.noaa.gov/explorations/12midatlantic/logs/aug26/aug26.html) and others off Nantucket at 1100–1400 m (Quattrini et al., 2016). It is quite possible that the original specimens of *L. atlantis* and *L. blakeana* dredged from the edge of the continental shelf off Maryland and North Carolina (Figure 33) respectively might have been associated with cold seeps. Certainly, the latter species was recovered in the vicinity of extensive methane venting from the Blake Ridge gas hydrate province (Brothers et al., 2013). Similar sites of methane leakage are likely at the edge of the continental shelf off southern Newfoundland but there have been no biological surveys published, and, although it is possible that *L. thula* samples were trawled from such a site, we have no direct evidence. Cosel (1986) listed the macrofauna from the ERHAPS 851 survey but gave no details of individual stations; of 45 bivalve species recorded two other possible chemosymbiotic bivalves are *Solemya borealis* Totten, 1834 and *Thyasira* sp. (not all species harbour symbionts) but it is uncertain whether or not they co-occurred with *L. thula*.

Further to the south in the Gulf of Mexico several *Lucinoma* species have been reported associated with hydrocarbon seeps including putative *L. atlantis* (MacDonald et al., 1990; Cordes et al., 2000). Incidentally, some *Lucinoma* sp. reported from the hydrocarbon seeps are now assigned to other genera namely *Jorgenia* and *Graecina* and classified in the Myrteinae rather than Codakiinae (Taylor and Glover, 2009). In the southern Caribbean, Gracia et al. (2012) reported three *Lucinoma* species (unnamed) from cold seeps at around 500 m off Colombia and, at depths of 230–800 off Guadeloupe, Taylor and Glover (2016) recorded two unnamed species from dead shells in poor condition.

Globally there is a strong association of *Lucinoma* species with seeps, as well as mud volcanoes and oxygen minimum zones. *Lucinoma myriamae* (Cosel, 2006) occurs at seep sites from 360 –425 m off West Africa (Sibuet and Vangreisheim, 2009); *Lucinoma taiwanensis* was described from an area of known hydrothermal activity off north Taiwan 205–650 m (Cosel and Bouchet, 2008), *Lucinoma yoshidai* is reported at Japanese seeps between 100–1000 m (Okutani and Hashimoto, 1997) and *Lucinoma anemiophila* from 780 m at a methane seep off southwestern Chile (Holmes et al., 2005). From the eastern Mediterranean, *Lucinoma kazani* was described from 1700 m deep mud volcanoes (Salas and Woodside, 2002; Olu-Roy et al., 2004) and *L. asaphaeus* from mud volcanoes in the Strait of Cadiz (Oliver et al., 2012). Additionally two species of *Lucinoma* are known from sediments in oxygen minimum zones; *L. aequizonata* from 400 –650 m off southern California (Cary et al., 1989; Zamorano and Hendrickx, 2012; Hendrickx et al., 2016) and *Lucinoma gagei* from southern Oman at 675–967 m (Oliver and Holmes, 2006). *Lucinoma aequizonata* (Dall, 1901) has a remarkable tolerance of anoxia being able to survive 262 days without oxygen (Arndt-Sullivan et al., 2008).



Figures 34–52. *Lucinoma* specimens from northern Gulf of Mexico. **34–35.** *Lucinoma filosa* (NHMUK20140794), interior and exterior of RV, SW of Marquesas Rock, Florida Keys, 24°20.62' N, 82°16.41' W, 185–195 m, L=35.5 mm. **36–38.** *Lucinoma blakeana* (USNM 64435), exterior of LV and interior of RV and LV, off Havana, Blake station 43, 24°08' N, 82°51' W, 821 m, L=22.3 mm. **39–40.** *Lucinoma "atlantis"* (USNM 637445), interior and exterior of RV, Gulf of Mexico, 27°50' N, 91°11' W, 375 m, L=38 mm. **41–43.** *Lucinoma "atlantis"* exterior of LV and interior of RV and LV, Garcia collection no 24039, off Louisiana, Bush Hill seep site in lease block Green Canyon 185, 27°46.904' N, 91°30.286 W, 546–555 m. L=48.6 mm. **44–46.** *Lucinoma atlantis* exterior of LV and interior of LV and RV, Garcia colln no 24039, Off Louisiana, Bush Hill seep site in lease block Green Canyon 185, 27°46.904 N, 91°30.286 W, 546–555 m, L=53.5 mm. **47–50.** *Lucinoma* sp. (MCZ), off Alabama, Viosca Knoll lease block 826, 29°09' N, 88°01' W, ca. 450 m (Figures 47–48, L=81 mm; 49–50, L=80 mm). **51–52.** *Lucinoma* sp. (USNM 706740), off Tortugas (no details), 347–512 m, L=46 mm.

The fossil history of *Lucinoma* also reveals an association with hydrocarbon seep habitats. Although *Lucinoma*-like lucinids first appeared in the early Cenozoic in shallow water Paleocene deposits (Taylor et al., 2011) maybe as a sister clade to *Saxolucina*, they have been associated with fossil deep-water hydrocarbon seeps since the Oligocene; for example, *L. hannibali* (Clark, 1925) (Kiel, 2010; Nesbitt et al., 2013) and in the Italian Miocene *Lucinoma perusina* (Sacco, 1901) (Moroni, 1966). Massive accumulations of *Lucinoma* shells are recorded at sites of fossil seeps in the Miocene and Pliocene of Japan with inferred palaeo-depths of 50–300 m (Majima et al., 2003, 2005).

Continuing discoveries of hydrocarbon seeps, gas hydrates, pockmarks, mud volcanoes (e.g., Cunha et al., 2013; Quattrini et al., 2015) shows that these habitats are abundant along the margins of continental shelves. The biological communities associated with many of these have yet to be investigated and the focus of the better known sites has concerned epifaunal or shallowly infaunal bivalves, *Bathymodiolus* and Vesicomyidae (Olu-LeRoy et al., 2007; Cordes et al., 2009) with deeper burrowing taxa such as *Lucinoma* less well sampled or studied. Improved sampling and accompanying molecular studies should clarify the confused taxonomy of the Gulf of Mexico and wider Caribbean *Lucinoma* species and their relationships to the more northerly species along the eastern USA continental margin. From the research activity at hydrocarbon seeps in the northern Gulf of Mexico relatively few *Lucinoma* samples have been archived in museum collections despite their apparent abundance, as evidenced for example by Callender and Powell (1997).

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LITERATURE CITED

Abbott, R.T. 1974. American Seashells. 2nd edition. Van Nostrand-Reinhold, New York, 663 pp.

Arndt-Sullivan C, J- Lechaire, and H. Felbeck. 2008. Extreme tolerance to anoxia in the *Lucinoma aequizonata* symbiosis. Journal of Shellfish Research 27: 119–127.

Bretsky, S.S. 1976. Evolution and classification of the Lucinidae (Mollusca; Bivalvia). Palaeontographica Americana 8(50): 219–337.

Britton, J.C. 1970. The Lucinidae (Mollusca: Bivalvia) of the Western Atlantic Ocean. PhD dissertation George Washington University. University Microfilms 71–12, 288, 566 pp.

Brothers, L.L., C.L. Van Dover, C.R. German, C.L. Kaiser, D.R. Yoerger, C.D. Ruppel, E. Lobecker, A.D. Skarke, and J.K.S. Wagner 2013. Evidence for extensive methane venting on the southeastern U.S. Atlantic margin. Geology 41(7): 807–810.

Bush, K.J. 1886. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), and in the Caribbean Sea, (1879–80), and along the Atlantic Coast of the United States (1880) by the U. S. Coast Survey Steamer "Blake", Lieutenant-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XV. Report on the Mollusca dredged by the "Blake" in 1880, including descriptions of several new species. Bulletin of the Museum of Comparative Zoology 23: 194–244.

Callender, W.R., G.M. Staff, E.N. Powell, and I.R. MacDonald. 1990. Gulf of Mexico Hydrocarbon Seep Communities V. Biofacies and Shell Orientation of Autochthonous Shell Beds below Storm Wave Base. Palaios 5: 2–14.

Callender, W.R. and Powell, E.N. 1997. Autochthonous death assemblages from chemautotrophic communities at petroleum seeps: palaeoproduction, energy flow and implications from the fossil record. Historical Biology 12: 165 –198.

Callender, W.R. and Powell, E.N. 2000. Long-term history of chemautotrophic clam-dominated faunas of petroleum seeps in the northwestern Gulf of Mexico. Facies 4: 177 –204.

Cary, S.C., B. Fry, H. Felbeck, and R.D. Vetter. 1989. Habitat characterization and nutritional strategies of the endosymbiont-bearing bivalve *Lucinoma aequizonata*. *Marine Ecology – Progress Series* 55: 31–45.

Chavan, A. 1938. Essai critique de classification des lucines. Compléments. Journal de Conchyliologie 82(3): 215–241.

Chavan, A. 1969. Superfamily Lucinacea Fleming, 1828. In: Moore, R.C., (Ed.) Treatise on invertebrate paleontology, Part N, Mollusca 6, Bivalvia, vol. 2., Geological Society of America and University of Kansas Press, Boulder, Colorado. pp. N491–N518.

Clark, B.L. 1925. Pelecypoda from the marine Oligocene of western North America. University of California Publications in Geological Science 15: 69–136.

Coan, E.G., P. Valentich-Scott, and F.R. Bernard. 2000. Bivalve seashells of Western North America, Marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History, 764 pp.

Cordes, E., D.C. Berguist, and C.R. Fisher. 2009. Macro-Ecology of Gulf of Mexico Cold Seeps. Annual Review of Marine Science 1: 143–68.

Cosel, R. von. 1986. Buccins.... cones des eaux froides. Compte-rendu succinct de la campagne ERHAPS 851 à St.-Pierre-et-Miquelon. Xenophora 32: 10–16.

Cosel, R. von. 2006. Taxonomy of West African bivalves VIII. Remarks on Lucinidae, with descriptions of five new genera and nine new species. Zoosystema 28: 805–851.

Cosel, R. von and P. Bouchet. 2008. Tropical deep-water lucinids (Mollusca: Bivalvia) from the Indo-Pacific: essentially unknown, but diverse and occasionally gigantic. In: Héros, V., Cowie, R.H. and Bouchet, P. (Eds), Tropical Deep Sea Benthos 25. Mémoires du Muséum national d'Histoire naturelle 196: 115–213.

Cunha, M. R., C. F. Rodrigues, L. Génio, A. Hilário, A. Ravara, and O. Pfannkuche. 2013. Macrofaunal assemblages from

mud volcanoes in the Gulf of Cadiz: abundance, biodiversity and diversity partitioning across spatial scales, Biogeosciences, 10: 2553–2568.

Dall, W.H. 1901. Synopsis of the Lucinacea and of the American species. Proceedings of the United States National Museum 23: 779–833.

Distel, D.L. and H. Felbeck. 1987. Endosymbiosis in the lucinid clams *Lucinoma aequizonata*, *Lucinoma annulata* and *Lucina floridana*: a rexamination of the functional morphology of the gills as bacteria-bearing organs. Marine Biology 96: 79–86.

Duperron, S., A. Fiala-Medioni, J.C. Caprais, K. Olu, and M. Sibuet. 2007. Evidence for chemoautotrophic symbiosis in a Mediterranean cold seep clam (Bivalvia: Lucinidae): comparative sequence analysis of bacterial 16S rRNA, APS reductase and Rubis CO genes. FEMS Microbiology and Ecology 59: 64–70.

Fleming, J. 1828. A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca and Radiata of the United Kingdom; including the indigenous, extirpated and extinct kinds; together with periodical and occasional visitants. Bell & Bradfute, Edinburgh, 565 pp.

Glover, E.A. and J.D. Taylor. 2016. Lucinidae of the Philippines: highest known diversity and ubiquity of chemosymbiotic bivalves from intertidal to bathyal depths (Mollusca: Bivalvia). *In:* Héros, V., Strong, E. and Bouchet, P. (Eds). Tropical Deep-Sea Benthos 29. Mémoires du Muséum national d'Histoire naturelle 208: 65–234.

Gracia, A., N. Rangel-Buitrago, and J. Sellanes. 2012. Methane seep molluscs from the Sinu-San Jacinto fold belt in the Caribbean Sea of Colombia. Journal of the Marine Biological Association of the United Kingdom, 92: 1367–1377.

Habe, T. 1958. Report on the Mollusca chiefly collected by the S.S. Sôyô-Maru of the Imperial Fisheries Experimental Station on the continental shelf bordering Japan during the years 1922–1930. Publications of the Seto Marine Biological Laboratory 7: 19–52.

Hendrickx, M.E., P. Valentich-Scott, and N.Y. Suárez-Mozo. 2016. Deep-water bivalve mollusks collected during the TALUD XV cruise off the west coast of the southern Baja California Peninsula, Mexico. Biodiversity Data Journal 4: e8661.

Holmes, A.M., P.G. Oliver, and J. Sellanes. 2005. A new species of *Lucinoma* (Bivalvia: Lucinoidea) from a methane gas seep off the southwest coast of Chile. Journal of Conchology 38: 673–682.

Huber, M. 2015. Compendium of bivalves 2. ConchBooks, Harxheim, Germany. 907 pp.

Iredale, T. 1937. The Middleton and Elizabeth Reefs, South Pacific Ocean. Mollusca. Australian Zoologist 8: 232–261.

Kiel, S. 2010. The fossil record of vent and seep mollusks. In: Kiel, S. (Ed.). The Vent and Seep Biota – from Microbes to Ecosystems. Topics in Geobiology 33, Springer. Heidelburg. pp. 255–277.

MacDonald, I.R., N.L. Guinasso, J.F. Reilly, J.M. Brooks, W.R. Callender, and S.G. Gabriellae. 1990. Gulf of Mexico hydrocarbon seep communities: VI. Patterns in community structure and habitat. Geo-Marine Letters 10: 244–252.

McLean, R.A. 1936. A new deep-water *Lucina* from off Maryland. The Nautilus 49: 87.

Majima, R, K. Ikeda, H. Wada, and K. Kato. 2003. An outer-shelf cold-seep assemblage in forearc basin fill, Pliocene Takanabe Formation, Kyushu Island, Japan. Paleontological Research 7: 297–311.

Majima, R., T. Nobuhara, and T. Kitazaki. 2005. Review of fossil chemosynthetic assemblages in Japan. Palaeogeography, Palaeoclimatology, Palaeoecology 227: 86 –123.

Moroni, M.A. 1966. Malacofauna del 'Calcare a Lucine' di S. Sofia-Forli. Palaeontologia Italica 60: 69–87.

Nesbitt, E.A., R.A. Martin, and K.A. Campbell. 2013. New records of Oligocene diffuse hydrocarbon seeps, northern Cascadia margin. Palaeogeography, Palaeoclimatology, Palaeoecology 390: 116–129.

Okutani, T. and J. Hashimoto. 1997. A new species of lucinid bivalve (Heterodonta: Lucinidae) from Kanesu-no-Se bank near the mouth of Suruga Bay, with a review of the Recent species of the chemosynthetic genus *Lucinoma* from Japan. Venus 56: 271–280.

Oliver, P.G. and A.M. Holmes. 2006. A new species of *Lucinoma* (Bivalvia: Lucinoidea) from the oxygen minimum zone of the Oman margin, Arabian Sea. Journal of Conchology 39: 63–77.

Oliver, P.G., C.F. Rodrigues, and M.R. Cunha. 2012. Chemosymbiotic bivalves from the mud volcanoes of the Gulf of Cadiz, NE Atlantic, with descriptions of new species of Solemyidae, Lucinidae and Vesicomyidae. ZooKeys 113: 1–38.

Olu-Le Roy, K., M. Sibuet, A. Fiala-Médioni, S. Gofas, C. Salas, A. Mariotti, J.-P. Foucher, and J. Woodside. 2004. Cold seep communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. Deep-Sea Research I 51: 1915–1936.

Olu-Le Roy, K., J.-C. Caprais, A. Fifis, M.-C. Fabri, J. Galéron, H. Budzinsky, K. Le Ménach, A. Khripounoff, H. Ondréas, and M. Sibuet. 2007. Cold-seep assemblages on a giant pockmark off West Africa: spatial patterns and environmental control. Marine Ecology 28: 115–130.

Quattrini, A.M., M.S. Nizinski, J.D. Chaytor, A.W.J. Demopoulos, E.B. Roark, S.C. France, J. A. Moore, T. Heyl, P.J. Auster, B. Kinlan, C. Ruppel, K.P. Elliott, B.R.C. Kennedy, E. Lobecker, A. Skarke, and T.M. Shank. 2015. Exploration of the canyon-incised continental margin of the northeastern United States reveals dynamic habitats and diverse communities. PLoSONE 10(10): e0139904.

Reeve, L.A. 1850. Monograph of the genus *Lucina* Pls V –XI. *Conchologica Iconica, Volume 6*. Reeve, Benham & Reeve, London.

Sacco, F. 1901. I Molluschi de Terreni Terziarii del Piemonte e della Liguria. Part 29. C. Clausen, Torino. 216 pp.

Salas, C. and J. Woodside. 2002. *Lucinoma kazani* n. sp. (Mollusca: Bivalvia): evidence of a living benthic community associated with a cold seep in the eastern Mediterranean Sea. Deep-Sea Research I 49: 991–1005.

Sibuet, M. and A.Vangriesheim. 2009. Deep-sea environment and biodiversity of the West African Equatorial margin. Deep-Sea Research II, 56: 2156–2168.

Skarke, A., C. Ruppel, M. Kodis, D. Brothers, and E. Lobecker. 2014. Widespread methane leakage from the seafloor on the northern US Atlantic margin. Nature Geoscience 7: 657–661.

Stimpson, W. 1851. Shells of New England; a revision of the synonymy of the testaceous mollusks of New England. Phillips, Sampson & Co., Boston. 58 pp.

Taylor, J.D. and E.A. Glover. 2009. New lucinid bivalves from hydrocarbon seeps of the Western Atlantic (Mollusca: Bivalvia: Lucinidae). Steenstrupia, 30: 127–140.

Taylor, J.D. and E.A. Glover. 2010. Chemosymbiotic bivalves. In: Kiel, S., (Ed.) The Vent and Seep Biota – from Microbes

to Ecosystems. Topics in Geobiology, 33. Springer Heidelburg. pp. 107–135.

Taylor, J.D. and E.A. Glover. 2016. Lucinid bivalves of Guadeloupe: diversity and systematics in the context of the tropical Western Atlantic (Mollusca: Bivalvia: Lucinidae). Zootaxa 4196(3): 301–380.

Taylor, J.D., E.A. Glover, L. Smith, P. Dyal, and S.T. Williams. 2011. Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). Zoological Journal of the Linnean Society 163: 15–49.

Taylor, J.D., E.A. Glover, and S.T. Williams. 2014. Diversification of chemosymbiotic bivalves: origins and relationships of deeper water Lucinidae. Biological Journal of the Linnean Society 111: 401–420.

Taylor, J.D., E.A. Glover, L. Smith, C. Ikebe, and S.T. Williams. 2016. New molecular phylogeny of Lucinidae: increased taxon base with focus on tropical western Atlantic species (Mollusca: Bivalvia). Zootaxa 4196(3): 381–398.

Theroux, R B. and R.L.Wigley. 1998. Quantitative composition and distribution of the macrobenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States. U.S. Department of Commerce. NOAA Technical Report, NMFS 140, 240 pp.

Totten, J.G. 1834. Description of some new shells belonging to the coast of New England. American Journal of Science 26: 366–369.

Turner, R.D. 1985. Notes on mollusks of deep-sea vents and reducing sediments. American Malacological Bulletin, Special Edition 1: 23–34.

Wigley, R.L. and R.B. Theroux. 1981. Atlantic continental shelf and slope of the United States -macrobenthic invertebrate fauna of the Middle Atlantic Bight Region - faunal composition and quantitative distribution. U.S. Geological Survey Professional Paper, 529-N: N1–N198.

WoRMS World Register of Marine Species. http://www.marinespecies.org.

Zamorano, P. and M.E. Hendrickx. 2012. Distribution of *Lucinoma heroica* (Mollusca: Bivalvia: Lucinidae) in the minimum oxygen zone in the Gulf of California, Mexico. Marine Biodiversity Records 5: 1–8.